THE CONNECTIONS OF THE GONADIAL BLOOD VESSELS AND THE FORM OF THE NEPHRIDIA IN THE ARENICOLIDÆ.

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The gonads of *Arenicola* occur on certain blood vessels that lie diagonally on the exterior of the glandular portion of the nephridia and that are consequently designated the gonadial vessels. In a study of the gonads, the results of which will be published shortly, it was found that the literature of the subject contained conflicting and inaccurate statements regarding the relations of these gonadial vessels to their connecting vessels. This paper is the result of an attempt to determine these relations.

Gamble and Ashworth, in 1900, published an extended study of the anatomy of the several species which also reviewed the important literature on the family. They had previously published, 1898, a paper on the anatomy of *Arenicola marina*. In an article published in 1899, V. Willem disagreed with some of their statements as did R. Lillie in a more recent publication, 1906. These contradictory statements I shall try to adjust: I must also take exception to some other statements of each.

The general relations of the blood vessels may be easily understood from the accompanying partly diagrammatic figure of a cross-section at about the level of the first nephridium of *A. cristata* (Fig. 1). It will be noted that there are two main blood vessels, a dorsal and a ventral; these run the entire length of the animal. There is a pair of neurals of much smaller caliber, also extending the full length of the body. The paired gastric laterals and subintestinals, as also the paired integumentary vessels known as the parietal (or dorsal longitudinal) and the longitudinal nephridial, are limited in their extent and vary in length and prominence in the several species.

All previous authors agree in the arrangement of the nephridial vessels as follows: The afferent vessel, on approaching the

nephridium, divides, one branch going to the setal sac and gill, if present, one to the integumentary vessels and one to the nephridium. The latter enters the nephrostome and forks, one branch traversing each lip. After reuniting, the vessel, reformed, runs out onto the wall of the nephridium as the gonadial vessel. Each of the three main branches of the afferent vessel gives off smaller vessels which, with more or less anastomosing with adjacent vessels, form capillary net-works in the organs supplied.

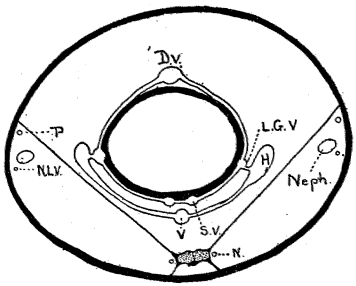


FIG. 1. Partly diagrammatic cross-section of *Arenicola cristata* at about the level of the first nephridium. *D. V.*, dorsal blood vessel. *H.*, heart. *L. G. V.*, lateral gastric blood vessel. *N.*, neural blood vessel. *N. L. V.*, nephridial longitudinal blood vessel. *P.*, parietal blood vessel. *S. V.*, sub-intestinal blood vessel. *V.*, ventral blood vessel.

The efferent vessels are formed by the union of capillaries in these same regions.

The afferent vessel, as a rule, comes from the ventral vessel. This is true for all except the first two nephridia of *A. Grubii* and of *A. ecaudata*, which nephridia are supplied, the first by a branch of the dorsal, the second by a branch of the parietal vessel (Fig. 2, *d*). In addition to the afferent vessel from the ventral vessel, the following nephridia also receive branches from the dorsal vessel: the first of *A. cristata*, the first two of *A. Claparedii* and the first three of *A. marina* (Fig. 2).

The following nephridia return blood directly to the subintestinal vessels through efferent vessels whose numerous branches are adjacent to their funnels: the fourth, fifth and sixth of *A. cristata*, the fourth and fifth of *A. Claparedii* and the fifth and sixth of *A. marina*. All others must pour the blood into the parietal and nephridial longitudinal vessels which, in turn, pass it to some of the more posterior efferent vessels (Fig. 2).

These observations are directly antagonistic to those of other investigators on several points of anatomical detail and of function of some of the vessels. I have given above a statement of the general arrangement of the branching afferent vessels with reference to the nephridia; it will be evident from text-figure 2 that my results only agree in a general way with the statements

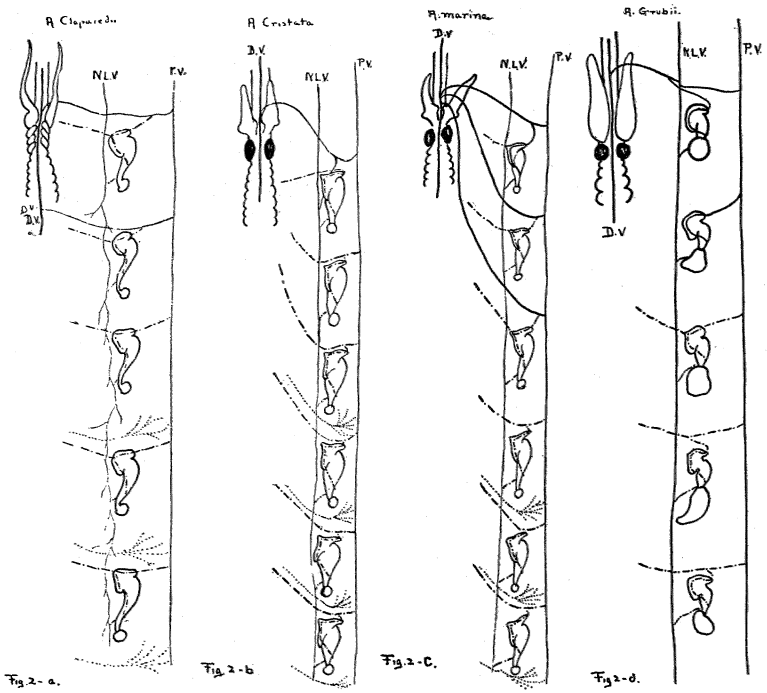


FIG. 2. Diagrams of the blood vessels supplying the nephridia in the several species of *Arenicola*, *a*, *A. Claparedii*, *b*, *A. cristata*, *c*, *A. marina*, *d*, *A. Grubii*; *d* will also serve as a diagram of the blood vessels of *A. ecaudata*. The form of the nephridia and of the digestive organs in the latter species, would be somewhat different but the arrangement of the blood vessels is the same as in *A. Grubii*. The dorsal vessel is shown by a solid line, thus ___. Afferent vessels arising from the ventral vessel are shown in broken lines, —.—.—. Efferent vessels connecting with the sub-intestinal blood vessel are shown in dotted lines, ... *D. V.*, dorsal vessel. *N. L. V.*, nephridial longitudinal vessel. *P. V.*, parietal blood vessel.

of previous authors. Thus in all nephridia of *A. Claparedii*, in some of *A. marina* and occasionally in *A. Grubii*, the afferent branch of the ventral vessel enters the *apex* of the funnel before it branches. In *A. cristata* one finds frequently, particularly in the somites containing the second and third nephridia, that the affer-

ent vessel gives off no branches to the nephridia, but the latter are supplied by a branch from the parietal.

The branch of the dorsal vessel to the second nephridium is small in *A. Claparedii*, but functional still. Gamble and Ashworth show and describe an afferent vessel to the first nephridium of *A. marina;* with this V. Willem disagrees, showing for this nephridium only a branch from the dorsal. In the majority of cases I find a branch from the ventral vessel also, thus agreeing with Gamble and Ashworth; in a few animals it is apparently wanting. I do not find, however, the efferent vessel from the fourth nephridium, in *A. marina*, to the subintestinal, which Gamble and Ashworth show but which V. Willem claimed was not present.

It is not true that the three main branches of the afferent vessel break up into capillaries; the one to the setal sac and gill does. The one to the integumentary vessels unites with them. The branch which enters the funnel continues as the gonadial vessel, runs peripherad to the nephridium and connects with the nephridial longitudinal, except in *A. Claparedii.*

The parietal and nephridial longitudinal vessels are distinct throughout the nephridial region in *A. Grubii*, *A. ecaudata* and *A. marina.* In *A. cristata*, the parietal is distinct but the nephridial longitudinal, while large at the level of the first nephridium, tapers posteriorly, becoming obscure back of the third nephridium. The parietal vessel is distinct the entire length of the nephridial region in *A. Claparedii.* The statement of Gamble and Ashworth that it is absent in this form is only explicable because they worked on preserved material; it is plainly evident in the living worm. The nephridial longitudinal, as a distinct vessel, is absent in this form except in the region of the first nephridium: its place is taken by a series of small connecting vessels, as if the gonadial vessel branched and some of its branches ran back to connect with those of the next posterior gonadial vessel.

In all cases the branches of the dorsal vessel running to the nephridia are afferent vessels. Gamble and Ashworth state that "The first nephridia of A. Grubii and A. ecaudata are *supplied* by a branch from the dorsal vessel" (the italics are mine), yet "The first three nephridia of A. marina, the first two of A. Clapa-

redii and the first of A. cristata *return* blood to the dorsal vessel." On *a priori* grounds, it would be strange to find the homologous blood vessels in closely related species carrying blood in opposite directions. I am certain that in *A. cristata* the blood flows from the dorsal vessel out to the parietal, the nephridial longitudinal vessel and to the nephridium, in this branch of the dorsal vessel. In this species the individuals are so large that in chloretonized specimens the direction of the blood movement is seen with comparative ease. S. E. Keith who has worked carefully for some time on the circulation of *A. cristata* gives me permission to quote her on this point as follows: "I have referred to these blood vessels in my own notes as the third pair of branches of the dorsal vessel. Gamble and Ashworth speak of the dorsal as receiving these branches, but the blood flows outward in them I am sure."

I have watched the blood-flow in *A. Claparedii;* the skin is frequently so transparent it may be seen without dissection. The flow is certainly away from the dorsal vessel in this species also. I am reasonably certain that such is the case in *A. marina,* in chloretonized specimens of which I have watched the blood movement. In this opinion I am supported by Willem who says of *marina,* "Il faut remarquer de plus, au point fonctionnel, que le sang circulant dans le tronc dorsal d'arriere en avant, le contenu des trois branches qui en emanent progresse dans une direction centrifuge."

Lillie makes the statement that "The vessel (segmental) begins its formation at the junction with the subintestinal blood vessel. Near its junction with the body wall the main vessel (segmental) gives off a branch (the nephrostomial vessel) which curves back, passes inward and barkward along the dorsal lip of the nephrostome." From this quotation it is evident that Lillie traces the afferent nephridial vessel to the subintestinal blood vessel, while, as stated above, I trace it, in agreement with Gamble and Ashworth and other observers, to the ventral vessel. The contradiction is only verbal, not real, for Lillie, in the explanation of his figures, labels this subintestinal vessel "the subintestinal *or* ventral vessel," a usage which he gets from oligochæt anatomy and which is incorrect here. Lillie finds that in *Arenicola* as in

other *Polychæta*, (see Fraipont on *Poygordius*, for instance), as well as in the *Oligochæta* (Wilson on *Lumbricus*), the first vessel to arise as a differentiation of the mesoderm, is the ventral vessel. Wilson says "The first vessel to appear (in *Lumbricus*) is the ventral or subintestinal." What the relation of this first vessel genenally is to the development of the circum-intestinal network in the polychæts is an unsettled point. (See Edward Myer's "Studien über den Körperbau der Anneliden," III., p. 464.) Recently Schiller writes as follows: "Nur bezuglich Blutsinus und Darmgefäsznetz ist mann bei *Arenicola Grubii* noch nicht ins klare gekommen, welches von den beider das primäre sei, da verscheidene Autoren ganz verscheidener Ansicht daruber sind. Die einer behaupten dasz zuerst der Sinus auftrete und sekundär sich in ein Netz auflöse: die anderen bezeichnen den Blutsinus als ein Produkt des zusammengeschmolzen Darmgefäsznetzes." He does not care to express an opinion on the subject although of the growing posterior region of *A. Grubii* he says: "Im Darmepithel keine besonderen Zellen vorkommen, die Antrit an der Bildung eines Sinus nehmen könnten." In considering der Blutsinus, Darmgefäsznetz und Subintestinalgefäsz he says: "Diese drei Gebilde werden hier zusammen als anatomisch und entwickelungsgeschichtlich zusammengehörende Elemente."

I have taken pains to quote in order to show that in spite of the difference of opinion regarding the origin of the network of intestinal vessels there is no tendency to include the ventral vessel in *Arenicola* or other polychæts as a part of this network which does, however, include the subintestinals. In *A. marina* we know (Benham, 1893) that the subintestinal vessels and the gastric longitudinals develop as the result of a fusion of the walls of the circular vessels of the alimentary canal. While in the oligochæts the subintestinal vessels split off from the ventral vessel. (Beddard, F. E., "Monograph of the Oligochæta," p. 70.) The term subintestinal vessel is an incorrect term for the vessels so named in *Arenicola*. Lillie should not have used the term subintestinal when he meant ventral, as these two terms are not interchangeable in *Arenicola*. The ventral vessel or subintestinal vessel of *Lumbricus* — they remain united in this form — is not homologous to the ventral plus the subintestinal vessels of *Arenicola*.

There is need of amendment in the description and figures of the form of the nephridia of the genus. The funnels, in particular, are much more symmetrical, in some species, than they have heretofore been shown. The usual technique is at fault in distorting them. The funnels are attached to the oblique muscles in *A. Claparedii*, *A. cristata* and *A. marina*. When the worm is opened and pinned out for dissection, the strain on these oblique muscles or on the connecting blood vessels of the other species, pulls the funnels throughly out of shape. It is, therefore, well to stupefy the worm by adding, drop by drop, seventy per cent. alcohol to the smallest quantity of sea water that will cover the worm in a long narrow dish. Then when the muscular walls are relaxed, the body cavity is injected by means of a hypodermic syringe or a fine pipette, until the walls are well distended with

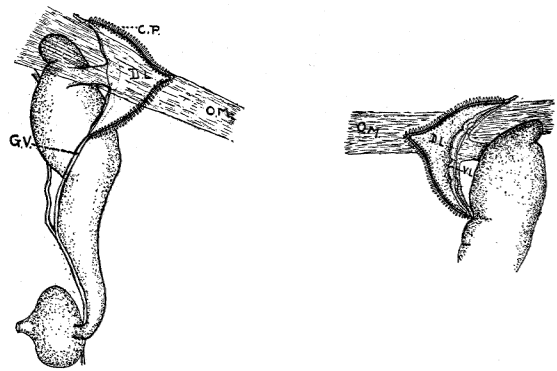


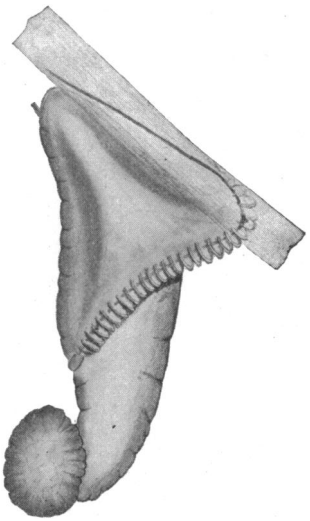
FIG. 3. Dorsal view of the second left nephridium of *Arenicola cristata*, × 3. *C.P.*, ciliated plates. *D.L.*, dorsal lip. *G.V.*, gonadial blood vessel. *O.M.*, oblique muscle.

FIG. 4. Ventral view of the anterior portion of second left nephridium of *Arenicola cristata*, × 3. *D.L.*, dorsal lip. *V.L.*, ventral lip.

the fixing agent. (Kopsch fluid answers well.) The whole worm is then placed in the fixing fluid. The nephridia are thus hardened without distortion and when dissected out later show their proper form.

The figures of the funnels or entire nephridia of each of the species are shown in the accompanying figures. The funnel of *A. cristata* (Figs. 3 and 4) is the most complicated and at the same time the most symmetrical in the genus. It is flattened, with a broadly sagittate or hastate form. Its dorsal lip,

which is attached by its outer surface to the oblique muscle, forms the point of the arrow. The ventral edge of this lip is set with from thirty to sixty ciliated plates which stand nearly at right angles both to the plane of the lip and to its edge. A loop of the blood vessel which traverses the dorsal lip runs up into each plate. The ventral lip is bow-shaped and divided into three segments like the handle and ends of a bow; the convexity of the bow turns toward the apex of the dorsal lip. The opening of the nephrostome is a long narrow slit between the base of the triangular dorsal lip and the bow-shaped ventral lip; the opening leads into the rapidly narrowing throat. The hastate funnel is held to the body by a short slender haft; the body of the nephridium, the glandular portion, is club-shaped; the funnel attaches to its side near the larger end, the axis of the



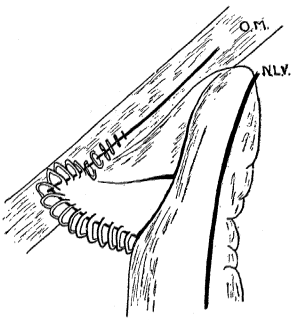


FIG. 5. Dorsal view of a nephridium of *A. marina*, × 15.

FIG. 6. Ventral view of the anterior end of the nephridium of *Arenicola marina*, × 15. *N.L.V.*, nephridial longitudinal blood vessel. *O.M.*, oblique muscle.

funnel being nearly at right angles to the longitudinal axis of the body. The body of the nephridium joins the roughly spherical bladder at the smaller end of the body, the handle of the club. The bladder opens to the exterior on its peripheral side by a very short duct leading to the nephridiopore.

The nephridium of *A. marina* approaches, at times, quite nea

to the form of that of *A. cristata;* but usually it is quite different from it (Figs. 5 and 6). The general shape of the body and of the bladder is nearly the same as in the nephridium of *A. cristata*, although in *A. marina* the body is more frequently curved while that of *A. cristata* is straight. The funnel shows great variation and often departs widely from the type of *A. cristata*. It is a flattened flap having roughly the shape of an equilateral triangle. At one angle the funnel opens into the anterior end of the body of the nephridium; along the opposite side lies the nephrostome. One of the sides adjacent to the neck is attached to the oblique muscle; the other adheres to the margin of the body. The axis of the funnel forms, therefore, an angle of only thirty or so degrees with the axis of the body. The dorsal lip is straight or slightly concave; it is set with twenty five or thirty somewhat lanceolate ciliated plates, each of which is supplied with a loop of the blood vessel. The ventral lip, Fig. 6, is regularly concave.

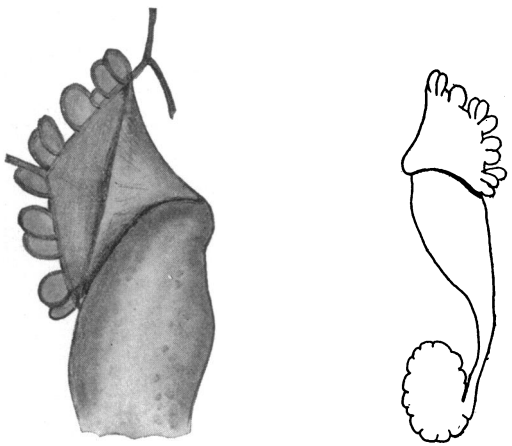


FIG. 7. Ventral view of the anterior portion of the third left nephridium of *Arenicola Claparedii*, × 30.

FIG. 8. Dorsal view of the nephridium of *Arenicola Claparedii*, × 15.

The ciliated plates which run along the edge of the dorsal lip, tend to continue along the blood vessel past the angle which the dorsal lip makes with the side of the funnel that attaches to the oblique muscle. This blood vessel runs along the muscle nearly parallel with the edge of the funnel. There are from ten to twenty of these plates; those along the blood vessel on the muscle

diminish in size. When occasionally there are an unusally large number of them along the blood vessel beyond the angle, the angle of the funnel adjacent to the muscle tends to become the apex of the funnel as in *A. cristata*, and the mouth shifts so as to more nearly face this angle instead of a side. In such cases the throat of the funnel opens into the body some distance back of the anterior end of the latter.

The funnel of the nephridium of *A. Claparedii* (Figs. 7 and 8) is least complicated. If we imagine a simple funnel form with short stem to be flattened and to have one lip pulled out into a triangular protrusion, we may gain a clear idea of the funnel of this species. The apex of the dorsal lip is broadly obtuse; the ventral lip is straight. The dorsal lip is set with the ciliated plates characteristic of the *marina* section of the genus which, as Gamble and Ashworth point out, includes the species *Claparedii*, *cristata*

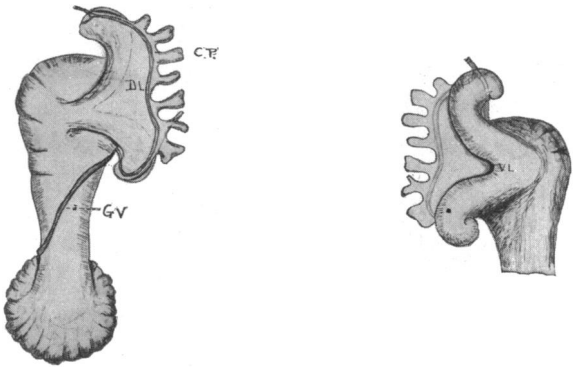


FIG. 9. Dorsal view of the first left nephridium of *Arenicola ecaudata*, × 15 *C.P.*, ciliated processes. *D.L.*, dorsal lip. *G.V.*, gonadial blood vessel.

FIG. 10. Ventral view of the anterior portion of nephridium (first left) of *A. ecaudata*, × 15. *V.L*, ventral lip.

and *marina*. There are ten or twelve of these plates in *A. Claparedii*. The funnel is at the anterior end of the body and its axis is also at right angles to the axis of the body of the nephridium.

The funnel of the nephridium of *A. ecaudata* (Figs. 9 and 10) is reniform in outline with revolute ends as seen from the ventral face. It also is flattened; the dorsal lip is slightly concave, the ventral lip is deeply indented. The dorsal lip is provided with ten to thirty blunt, at times much branched, finger-like processes;

these are covered with cilia, and within each is a blood sinus instead of a loop of the blood vessel. The throat of the funnel is relatively wide; the funnel attaches at the end of the body and usually has the customary position with its axis at right angles to the long axis of the nephridial body. Not infrequently however, the axis of the funnel is continuous with the axis of the body and we have a simple, unbent, tubular nephridium (Fig. 11). It is interesting to find such variation in this species for it makes evident how the more aberrant forms of the nephridium, such as occur in *A. marina*, are derived from a simple tubular type; just as a paper tube may be bent with its end at right angles to its major axis.

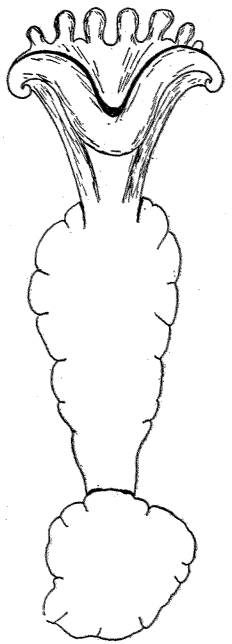
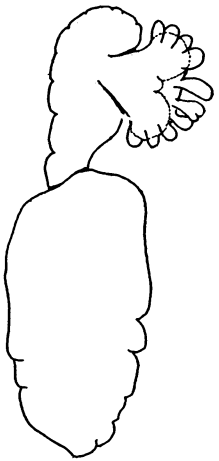


FIG. 11. An occasional form of the nephridium of *Arenicola ecaudata*, × 20.

A. Grubii (Figs. 12 and 13) possesses the same type of funnel as *A. ecaudata*. It is flattened; the dorsal lip is semicircular, the ventral lip trilobate, with a small median lobe and large lateral ones, thus making this lip deeply notched. Ten or twelve blunt, digitate, ciliated processes attach to the dorsal lip; these are often branched and are provided with the blood sinus. The funnel attaches to the body at some distance from the anterior end and its axis is at right angles to the axis of the body. The bladder of the nephridium of this species is usually expanded: it is capable of equally wide expansion in *A. ecaudata* but is more often found contracted. In the other species, the bladder is not so distensible although it is relatively large at times, especially when filled with eggs or sperm about to be discharged through the nephridiopore.

I have collected *A. cristata* and *A. marina* near Woods Hole, Mass., *A. marina*, *A. Grubii* and *A. ecaudata* in the bay at Plymouth, England, and have studied fresh *A. Claparedii* and *A. Grubii* at Naples. I wish to express my sincere thanks to the directors of the biological stations at these several places, who

have kindly placed at my disposal, material and facilities for the work, and to the Carnegie Institution whose table at Naples it was my pleasure to occupy.



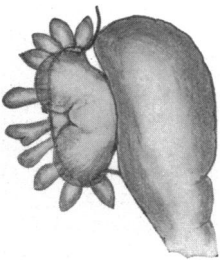


FIG. 12. The nephridium of *Arenicola Grubii*, × 15, dorsal view. The outline of the ventral lip of the funnel is shown in dotted line.

FIG. 13. Ventral view of anterior portion of the third left nephridium of *A. Grubii*, × 20.

BIBLIOGRAPHY.

Benham, W. B.

'93 Postlarval Stages of Arenicola marina. Jour. Mar. Biol. Ass. Plymouth, N. S., Vol. III., pp. 48–52.

Eisig, Hugo.

'98 Zur Entwickelungsgeschichte der Capitelliden. Mitth. Z. Stat. Neapel, Vol. XIII., pp. 1–293.

Fraipont, J.

'87 Le Genre Polygordius. Fauna u. Flora d. Golfes von Neapel, Vol. XIV., Monographie.

Freudweiler, Hedwig.

'05 Studien über das Gefäszsystem niederer Oligochaeten. Jen. Zeitschr. f. Naturwiss., Vol. XL., pp. 1–28.

Gamble, F. W., and Ashworth, J. H.

'98 Habits and Structure of Arenicola marina. Quar. Jour. Micr. Sci., Vol. XLI., pp. 1–42.

'00 The Anatomy and Classification of the Arenicolidæ. Quar. Jour. Micr. Sci., Vol. XLIII., pp. 419–569.

Lillie, Ralph.

'06 Structure and Development of the Nephridia of Arenicola cristata, Stimpson. Mitth. Z. Stat. Neapel., Vol. XVII., pp. 348–405.

Meyer, Ed.

'01 Studien über den Körperbau der Anneliden, III. Mitth. Z. Stat. Neapel., Vol. XIV., pp. 247–585.

Schiller, Ignaz.

'07 Ueber den feineren Bau der Blutgefässe bei den Arenicoliden. Doctor's Thesis, Univ. Zurich, Jena.

Willem, Victor.

'99 L'Excretion chez l'Arenicola. Travaux de la Station Zoologique de Mincreux, Vol. VII.

Wilson, E. B.

'89 The Embryology of the Earthworm. Jour. of Morph., Vol. III., pp. 388–462.

Vejdovsky, Franz.

'05 Zur Hämocöltheorie. Zeit. f. wiss. Zool., Vol. LXXXII., pp. 80–170.